A COLUMELLA IN MARCHANTIA POLYMORPHA

J. E. CRIBBS

(WITH PLATES I, II)

Introduction

Marchantia polymorpha, because of its wide distribution and common occurrence, has long been used as a representative of the Marchantiaceae for laboratory study. The large number of sporophytes appearing upon a single receptacle gives excellent opportunity to obtain various stages of development without much difficulty. Notwithstanding the wide usage of this species and the abundant literature dealing with the development and anatomy of the Marchantiaceae, it appears that in the organization of the capsule the tendency to develop a columella has never been recorded.

In the work of LEITGEB,[1] KIENITZ-GERLOFF,[2] and others observations are given on the development of the elaters within the capsule; and in each case these have been found to be irregularly disposed, appearing as elongated cells which are at first quite indistinguishable from the sporogenous cells, but soon may be detected by their failure to develop transverse walls. The present paper is concerned with some unusual incidents which may occur in the organization and development of these sterile tissues.

The material from which these observations were made was collected during the first week of September 1914. It was taken from an exposed area which had been cleared during the previous fall and burned over. As is frequently the case in such instances, it developed here in dense formation during the following summer. My attention was first attracted to the appearance of columnar structures during the spring of 1915 while preparing material from this collection. Further study of a large quantity from this locality gave one additional instance of this type of organization.

[1] LEITGEB, HUBERT, Untersuchungen über die Lebermoose. Vol. 6. 1881.

[2] KIENITZ-GERLOFF, F., Vergleichende Untersuchungen über die Entwickelungsgeschichte des Lebermoossporogons. Bot. Zeit. **32**:161. 1874; **33**:777–782. 1875.

Because of the dryness of the season and the infringement of more advanced stages of vegetation it was impossible to secure additional material from this locality during the fall of 1916.

Investigation

Two stages were observed in the organization of a central column of sterile tissue within the capsule. Fig. 1 gives a conception of the extent of development in the simpler of these. It may be seen that the close assemblage of a large number of elaters in the center has resulted in almost complete sterilization there. It will be observed in this case, too, that the central column was not originally composed entirely of cells which developed elaters, but mixed with these were sporogenous cells which disorganized before they could form tetrads, leaving protoplasmic remains which take stains deeply. It is doubtful whether the disintegration of these is to be interpreted as a source of additional nutriment for those which remain, or is in any way to be associated with this behavior which is characteristic of members of the Jungermanniales. It seems rather to be an occurrence associated with the unusual, close development of sterile tissue, for it may be observed that immediately outside of this zone there is no such behavior. The capsule, in this instance, has developed to the point where the spores have become isolated from the tetrads, and the elaters are beginning to develop the spiral thickenings characteristic of their walls. These are laid down beneath the more or less spirally disposed protoplasm which is conspicuous at this stage. This columnar development is not the result of assembling the normal number of elaters into a central position, for the diffuse arrangement so characteristic of the species is still maintained in the rest of the capsule; nor is the number, excluding those in the central column, in any way reduced from the normal average.

In the second stage of development (figs. 2, 3) there has been a complete elimination of sporogenous cells, so that the columella is composed of sterile tissue only. The sporophyte in this case was less mature than that represented in fig. 1. The scattered elaters show an almost evenly distributed protoplasmic content which has not yet collected preliminary to the formation of the spiral thicken-

ing. The sporogenous cells are in the compact spore stage following the development of tetrads.

The columella, which at this stage is clearly defined, extends from the base of the capsule through more than three-fourths of its length. It is composed largely of elaters which diverge slightly at the free end. Intermingled with the elaters occur tissues developed from sporogenous cells which have elongated and divided transversely a number of times, but failed to reach the spore mother cell stage; thus remaining as elongated sterile chains of cells which will not develop into elaters, but may, as in fig. 1, completely disintegrate during the later history of the capsule, or in this more compact columella there may be but a partial disorganization. This type of structure, judging from its position and development, is suggestive of the elaterophore of *Pellia*. It has a less advanced state of organization, however, since there is no apparent tendency either to diminish the number of diffusely scattered elaters or to assemble them at the apex of the column.

Another phase in the development of sterile tissue within the capsule is met with in the group of cells which occur at the apex. The development of sterile cells at this point at once recalls the condition existing in *Aneura*. KIENITZ-GERLOFF refers to the development of two layers of sterile cells here. Examination of a large number of sporophytes, however, will show that there is considerable variation in the amount of this tissue, and also that it may be formed in different ways.

Fig. 4 represents a young sporophyte when the greater density of the protoplasm in the distal half is just becoming manifest. There has been no separation of sterile tissue at the apex up to this stage. In this instance two eggs have been developed in the venter, only one of which is seen to be developing an embryo. It would seem, from the fact that all the other eggs developed on this receptacle were fertilized and forming sporophytes, that the failure of this one to do so may be attributed to a potential sterilization which follows the initial development of the egg first fertilized, a response comparable perhaps to that of *Pellia* or *Pallavicinia*, where but one sporophyte regularly develops from a group of closely assembled archegonia.

When the sporophyte has attained the stage immediately preceding the invasion of the gametophytic tissue by the developing foot, the first isolation of cells which will contribute definitely to the apical group may sometimes be observed (fig. 5). The first isolation is suggested by the appearance of more pronounced cell walls. In the structure of the cells themselves at this stage there is usually no observable difference; but when once the foot establishes itself, and the sporogenous cells rapidly increase in density and begin elongation, these become more prominent because of their less density, their more conspicuous nuclei, and their failure to undergo elongation.

In most cases a single layer of cells is formed, cut off at this early stage, although occasionally two layers in addition to the wall cells will be found. These originally isolated cells are commonly carried forward at the apex as the sporogenous cells below them continue their elongation; and they generally compose all there is of sterile tissue here, but not uncommonly the amount is increased in one of two ways. The sporogenous initials may by periclinal divisions contribute to the mass just before the rapid series of anticlinal divisions which accompanies the broadening of the capsule and elongation of the sporogenous cells (fig. 7). Moreover, the bulk of sterile tissue may be increased by the division of wall cells near the apex (fig. 6). The contribution by this method is apparently very slight and less common than by the former. A third method by which the tissue may be increased in bulk would be by continued division of the sterile cells after their first isolation. Although this would seem a very probable occurrence, I was unable to observe any direct evidence of it. The apical end of a more mature sporophyte is shown in fig. 8. The sporogenous cells are in the tetrad condition, and the close association of the elaters with the sterile cap toward which they converge is very conspicuous.

Conclusions

In the Marchantiaceae, the first family of the Bryophytes in which there occurs any sterilization of potentially sporogenous tissues, the elaters are commonly diffusely arranged; but in

Marchantia they sometimes develop so abundantly in the center of the capsule as to produce a columella.

Intermingled with the elaters occurs considerable tissue derived from sporogenous cells which undergo elongation and divide frequently, giving rise to chains of cells. These fail to reach the spore mother cell stage, and may persist for a considerable time. They either partially or completely disorganize, however, about the time the elaters develop their wall thickenings.

The disintegration of these sporogenous cells is a feature limited to the columella, and apparently is not essentially a nutritive function, but is a condition arising from the close grouping of the central elaters.

A columella of this type strongly suggests the elaterophore of *Pellia*, and is an advancement in the organization of the sterile tissues of this family along the same line of development that regularly appears in members of the Anacrogynae.

That this unusual occurrence may be attributable directly to external factors is highly improbable; but should be considered the first stage in the tendency to break up the sporogenous mass, a feature very prominently displayed in the sporophyte as it increases in size and complexity.

The initial separation of sterile cells at the apex may occur even before the intrusion of the proximal part to form the foot, or it may first be recognized at the time of the initial elongation of the sporogenous cells.

The group of cells thus separated at the tip may be added to either by the division of the wall cells, or by periclinal walls in the elongating sporogenous cells.

This occurrence of a cap of sterile cells at the apex of the capsule is likewise a feature appearing prominently in members of the Anacrogynae, where in *Aneura* it bears attached elaters. The occasional appearance of three or four layers of sterile cells at the tip, and the convergence of the elaters, together with the close relation they frequently bear to this point, are further evidences of transitional features from the diffuse arrangement of elaters to a definite organized structure such as the elaterophore found in members of the Jungermanniales.

I wish to express my appreciation of the helpful criticism of Dr. W. J. G. LAND.

UNIVERSITY OF CHICAGO

EXPLANATION OF PLATES

Fig. 3, ×63; all others, ×450

FIG. 1.—Simple columella at time of separation of spores from tetrads, showing dense cluster of elaters and disorganized sporogenous tissue.

FIG. 2.—Columella immediately preceding thickening of elaters; composed largely of chains of sporogenous cells which failed to reach spore mother cell stage.

FIG. 3.—Median view of sporophyte giving topography.

FIG. 4.—Young sporophyte preceding isolation of sterile cap cells; unfertilized egg beside sporophyte.

FIG. 5.—First isolation of sterile cap cells preceding elongation of sporogenous cells.

FIG. 6.—Cap cells readily distinguished at time of invasion of foot; wall cells contributing to sterile cap group.

FIG. 7.—Unusually large mass of sterile cells, 4 deep at apex.

FIG. 8.—Close relation of radiating elaters to apical group, tetrad stage.